Sexual Modes in the Colonial Kamptozoan Genus *Barentsia*

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Abstract. Sexual mode in colonial animals is expressed at the zooid, colony, and genet level; all three must be characterized to understand sexuality in these animals. I carried out such an examination of the sexual mode of a colonial kamptozoan (entoproct), *Barentsia hildegardae*, at Friday Harbor, Washington. Calyces never contained both ovaries and testes, and colonies never contained both male and female calyces. Calyces and colonies (including replicate colonies from the same genet) monitored over two years did not change sex. These results suggest that *B. hildegardae* is comprehensively gonochoric. For comparison, I examined the sexual mode of five other species in the genus *Barentsia*. *Barentsia benedeni*, *B. conferta*, and *B. ramosa* also appear to be comprehensively gonochoric. *Barentsia discreta* is hermaphroditic at the colony level, with gonochoric calyces whose sex is environmentally determined, as noted by previous workers. *Barentsia aggregata* has simultaneously hermaphroditic calyces; this was reported by the authors who described it, but has escaped notice in subsequent reviews of kamptozoan biology. There are thus three contrasting modes of sex within the genus *Barentsia*. All three modes also occur in colonial cnidarians, and two of them are known in bryozoans, colonial hemichordates, and colonial urochordates. These disparate sexual modes may have evolved as adaptations to differing environmental conditions or population densities.

Introduction

Colonial animals display a diversity of sexual modes. Every colonial species can be examined at two levels, that of the zooid (the structure that is iterated to form a colony) and that of the colony. In many colonial species,

there can be multiple colonies per genet (genetic individual: all tissue derived mitotically from one zygote) produced early in development by polyembryony, or later by fragmentation or encapsulation. Such animals have three levels of organization: the zooid, the colony, and the whole multicolony genet. One way of classifying the sexual modes of colonial animals (Wasson and Newberry, 1997) is to designate each of the three organizational levels as gonochoric (G), sequentially hermaphroditic (S), or simultaneously hermaphroditic (H). According to this system, 10 modes of colonial sex are possible (Fig. 1), although only 5 have known examples among animals (Wasson and Newberry, 1997).

Few researchers investigating colonial animals have thoroughly examined the sexual mode of zooids, colonies, and whole genets of a single species. Many report only the sexual mode of the zooids, leaving uncertain the sexual mode of the colony or the whole genet. We cannot examine the ecology and evolution of mating systems in colonial animals if words such as gonochoric and hermaphroditic are used without specifying the level to which they apply. Furthermore, colonial animals have rarely been monitored over time, so it has been difficult to distinguish gonochorism from sequential hermaphroditism (hermaphroditism with discrete, separated periods of male and female maturity) at any level.

The purpose of this investigation was to describe thoroughly the sexual mode of one barentsiid kamptozoan (entoproct), *Barentsia hildegardae*, by examining all three levels of colonial organization and monitoring them over time. Barentsiids are small marine suspension feeders; barentsiid colonies superficially resemble those of hydroids. Cuplike calyces containing U-shaped guts and ringed by tentacles are borne on stalks arising from prostrate stolons. The calyx is the sexually reproductive unit of a barentsiid kamptozoan zooid, at sexual maturity containing testes, ovaries, or both. Although the kamptozoan

GENET	Gonochoric	Sequentially hermaphroditic			simultaneously Hermaphroditic					
COLONY	gonochoric	gonochoric	seq. hermaphroditic		gonochoric	seq. hermaphroditic		simultaneously hermaphroditic		
ZOOID	Gonochoric	Gonochoric	Gonochoric	Seq. herm.	Gonochoric		Seq. herm.	Gonochoric	Seq. herm.	sim. Herm.
mode	GgG	SgG	SsG	SsS	HgG	HsG	HsS	HhG	HhS	HhH

Figure 1. Ten potential sexual modes of colonial animals. The three-letter abbreviation for each represents the mode of the genet (first capital letter), the colony (lower case), and the zooid (second capital), respectively. Only modes GgG, SsS, HhG, HhS, and HhH have known examples among colonial animals (Wasson and Newberry, 1997).

zooid includes the stalk and stolon, I have limited attention in this study to the calyx, because the kamptozoan calyx is the zooidal element most comparable to the reproductive zooids of other colonial animals such as hydroids, bryozoans, and ascidians.

The sexual modes of most barentsiid kamptozoans have not been well characterized. It has been suggested that most or all kamptozoan species are hermaphroditic (Nielsen, 1989), and that colony-level hermaphroditism achieved by gonochoric calyces (mode HhG; Fig. 1) is the rule in the genus *Barentsia* (Emschermann, 1985, 1994). The only two studies that have carefully investigated sexual mode in this genus showed that *Barentsia discreta* has mode HhG (Mukai and Makioka, 1980; Emschermann, 1985). I was therefore surprised when my field observations of *Barentsia hildegardae* suggested that it might be gonochoric at the colony level (mode GgG; Fig. 1). I monitored calyces, colonies, and genets of *B. hildegardae* for more than one year to verify that the species was indeed comprehensively gonochoric.

For comparison, I also examined five other barentsiid species. The sexual modes of *Barentsia conferta* and *B. ramosa* were previously unknown; my data suggest that both species are comprehensively gonochoric (mode GgG). The literature regarding the sexual modes of *B. benedeni* (Foettinger, 1887; Ehlers, 1890; Mariscal, 1965; Emschermann, 1994) and *B. discreta* (Ehlers, 1890; Oka, 1895; Marcus, 1939; Mukai and Makioka, 1980; Emschermann, 1985) contains conflicting reports of both comprehensive gonochorism (GgG) and colony hermaphroditism (HhG). My results indicate mode GgG for *B. benedeni*, and mode HhG for *B. discreta*. Finally, my results confirm an earlier report (Johnston and Angel, 1940) of comprehensive hermaphroditism (mode HhH; Fig. 1) for *B. aggregata*.

Materials and Methods

Determining the sexual mode of Barentsia hildegardae

Barentsia hildegardae Wasson, 1997, endemic to the northeastern Pacific, is common in the San Juan Archipelago, Washington (Wasson, 1997). I examined a population of *B. hildegardae* growing on the floating dock at the University of Washington's Friday Harbor Laboratories (FHL), San Juan Island, Washington, and identified the sexual mode (G, S, or H) of calyces, colonies, and genets.

This species grows abundantly on solitary ascidians (especially *Pyura haustor*) living on the FHL dock, and each ascidian may be host to many colonies. To assess field patterns of sex distribution, I collected 40 ascidians from the dock between May and July 1993, and removed and sexed all *B. hildegardae* calyces from a single 2-cm^2 area on each ascidian. Because it was not possible to determine colony boundaries, these 2-cm^2 plots may have contained multiple colonies.

To monitor known colonies of *B. hildegardae* over time, I grew colonies on glass microscope slides and tracked them for one year. I removed small pieces of colonies from ascidians on the FHL dock and tied them to slides (one fragment per slide). These slides were placed in fenestrated plastic slide boxes; the boxes were enclosed in nylon mesh (knee-high stockings) to reduce fouling, and were hung with ropes (about 2 m long) from the dock. Within a few weeks, stolons had grown and attached these colony fragments to the slides. During April 1993, 130 such slide colonies were started from 20 ascidians. In May 1993, 7 of these colonies originating from 7 ascidians were chosen, and 10 new, replicate slide colonies were created from each one, making a total of 200 slides (the 130 original ones and 70 replicate slides of known genetic origin).

Slides were examined eight times between June 1993 and July 1994, about every 6 to 8 weeks. At each sampling date, slide boxes were brought into the laboratory for 1 week. Each slide was carefully cleaned with a fine paintbrush, and the number of female, male, and immature calyces was noted. The slide boxes were then enclosed in clean nylon stockings and returned to the FHL dock. From July 1994 to August 1995, the slides were left unattended off the floating dock. They were then reexamined in August 1995.

Other barentsiid species

Barentsia conferta Wasson, 1997, and *B. ramosa* (Robertson, 1900) are both endemic to the northeastern Pacific; both of these species are found primarily in the low intertidal zone of exposed coasts (Wasson, 1997). Between May 1991 and July 1995, I collected colonies of *B. conferta* from a rocky shelf and *B. ramosa* from under overhangs in the low intertidal zone at Natural Bridges State Beach, Santa Cruz, California. *B. conferta* grew mainly in dense aggregations on articulated coralline algae; *B. ramosa* grew in dense clumps on rocky overhangs. I examined a total of 48 aggregations (presumed colonies) of *B. conferta* and 33 aggregations of *B. ramosa*, counting male, female, and immature calyces.

Barentsia benedeni (Foettinger, 1887) is a cosmopolitan species, found in bays and harbors around the world (Wasson, 1997). In July 1993, I collected five mussels bearing colonies of *B. benedeni* from floating docks in Lake Merritt, Oakland, California. The calyces in these colonies were not sexually mature. I removed 30 small colony portions from the mussels and grew these fragments on glass slides on a sea table at Long Marine Laboratory, Santa Cruz, California. In February 1994, when 21 of these 30 colonies sexually matured, I examined and sexed all the calyces of each colony. I also examined and sexed a preserved colony of this species from Lake Merritt, in the collection of the California Academy of Sciences (#10510).

Barentsia discreta (Busk, 1886) is widely distributed in most of the world's oceans, in both deep and shallow waters (Wasson, 1997). In October 1994 I obtained two large colonies of *B. discreta* from Mission Bay, San Diego, California. The calyces were not sexually mature. I removed 10 small portions of one colony and 11 of the other and grew them on glass slides on a sea table at Long Marine Laboratory. In August 1995, when the calyces had sexually matured, I examined these 21 slide-grown colonies for the presence of male, female, and immature calyces. I also examined specimens of *B. discreta* in the collection of the Allan Hancock Foundation, University of Southern California. This material (57D/1–10) consisted of 10 whole mounts (slides) of colonies from California, Mexico, Ecuador, and Peru.

Barentsia aggregata Johnston and Angel, 1940, is a little-known species of Antarctic waters. I examined all the specimens of *B. aggregata* deposited in the South Australian Museum, Adelaide, by Johnston and Angel from collections of the BANZ Antarctic Research Expedition (1929–1931) at Macquarie and Heard Islands. This material (E944–946; 948–953; 2132, 2133, and unregistered specimens in the BANZARE collection) consists of 10 preserved (wet) colonies, 9 whole mounts (slides) of colonies, and 31 slides of sectioned calyces.

Results

Barentsia hildegardae

Every sexually mature calyx of *Barentsia hildegardae* was either male (Fig. 2a) or female (Fig. 2b); a calyx never contained both testes and ovaries. Furthermore, examination of thousands of calyces during the course of this study (in field samples and in slide-grown colonies) never revealed a calyx with ripe ovaries and degenerating testes, or vice versa.

Most 2-cm^2 plots on ascidians at Friday Harbor contained calyces mainly or entirely of one sex (Fig. 3a), although many plots contained calyces of both sexes. I was unable to determine how many colonies were growing in a single plot. In plots containing both sexes, I never observed male and female calyces growing along the same stolon.

Single colonies grown on slides always consisted of calyces of only one sex. Of the 200 slide colonies sampled eight times over one year, none was ever found with a mix of sexes. Furthermore, none of the 200 slide-grown colonies changed sex over the year (June 1993–July 1994) of monitoring. Although most of the 200 colonies were either dead or nearly so by the end of the second year, 31 colonies were sexually mature in August 1995. All of these were still the same sex as the original colony had been.

Over the yearlong sampling period, all 70 replicate colonies of seven genets remained the same sex as the original colonies they were taken from, regardless of size or age, and regardless of whether they were raised in boxes with colonies of the same or opposite sex. Furthermore, 17 replicate colonies representing four genets were still sexually mature at the end of the second year; all were still the same sex as their source colonies.

Colonies grown on glass slides and kept in jars of seawater in the laboratory under various food, water flow, and temperature levels (as part of growth experiments unrelated to the present study) also contained calyces of only a single sex, and did not change sex over the course of the three-month experiments.

Barentsia conferta, B. ramosa, and B. benedeni

Calyces of *Barentsia conferta* and *B. ramosa* always contained either testes or ovaries, never both. Aggregations of calyces of these species always consisted mainly or entirely of one sex (Fig. 3b, 3c). In aggregations that contained both sexes, male and female calyces were not randomly distributed. Instead, the aggregation consisted mostly of calyces of one sex, and the calyces of the opposite sex were limited to one patch or one region of the aggregation. Whenever I found an aggregation containing both sexes, I teased it apart and found that the male and
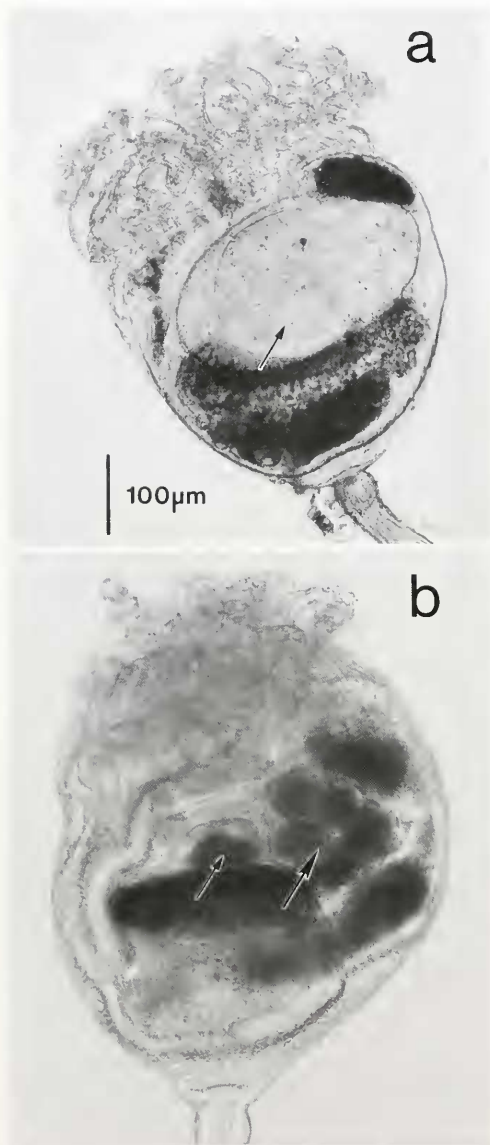
Figure 2. *Barentsia hildegardae.* (a) Male calyx in right-side view; right testis marked by arrow. (b) Female calyx in right-side view; right ovary marked by smaller left arrow; brood chamber containing embryos marked by larger right arrow. Scale bar applies to both a and b.

female calyces were growing on different stolons; I never observed male and female calyces growing on the same stolon.

Calyces of *Barentsia benedeni* contained either ovaries or testes, never both. Each of the 21 slide-grown colonies from Lake Merritt consisted of calyces of a single sex, although colonies did not contain very many sexually mature calyces (Fig. 3d). There were considerably more female than male colonies, probably because I had oversampled a single large female colony when originally removing colony portions from the mussels to generate the slide-grown colonies. The colony at the California Academy of Sciences (#105010) was huge and over-whelmingly female, consisting of about 950 female and 85 immature calyces (no male calyces were present); this colony is represented by the leftmost bar in Figure 3d.

Barentsia discreta

Calyces of *Barentsia discreta* (both museum and slide-grown colonies) contained either testes or ovaries, never both. In June 1995, when the slide-grown colonies first became sexually mature, only male (and immature) caly-ces were present. In July 1995, a few female calyces were present together with numerous male calyces in the same colonies. In August 1995, 11 of the 21 slide-grown colo-nies contained both male and female calyces at the same time, while 10 contained only male calyces; no colonies consisted only of female calyces (Fig. 3d). Five colonies in the collection of the Allan Hancock Foundation (57D/1, 3, 7, 8, 10) from California, Mexico, Ecuador, and Peru also had male and female calyces arising from the same stolon within a colony.

Barentsia aggregata

Many calyces in the South Australian Museum's col-lection of *Barentsia aggregata* from the Antarctic con-tained both ovaries and testes. Sectioned material (E2132) revealed particularly clearly the simultaneous presence in a single calyx of testes with ripe sperm, ovaries with yolky eggs, and a brood chamber with embryos. Although most preserved colonies consisted of calyces containing both ovaries and testes, a few contained only male or only female calyces.

Discussion

Comprehensive gonochorism (mode GgG): common in the genus Barentsia?

Of all the potential sexual modes for colonial animals (Fig. 1), mode GgG is the most difficult to demonstrate. To eliminate the possibility of sequential hermaphrodit-ism at any level, zooids, colonies, and genets must be monitored over time. To thoroughly exclude genet her-
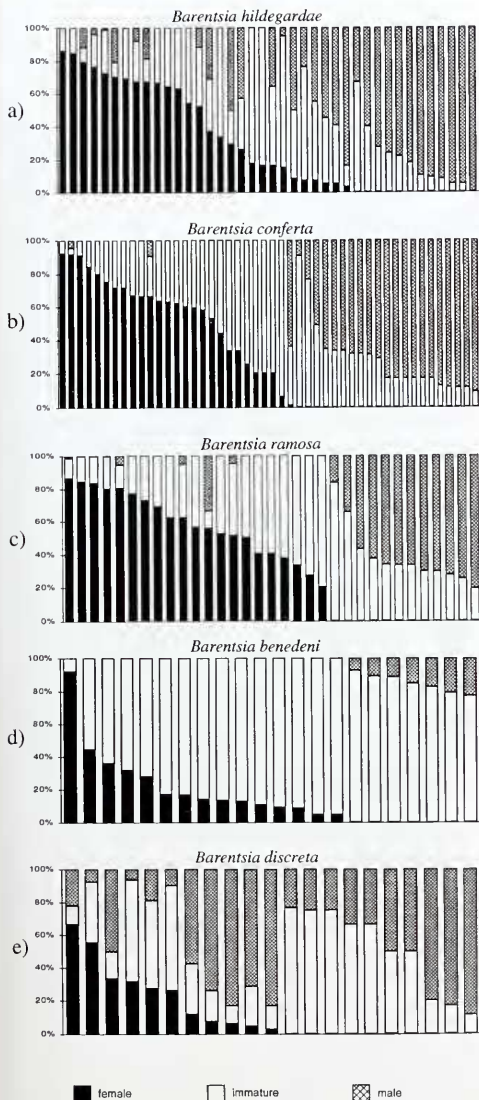
maphroditism, replicate colonies of the same genet must also be examined.

The data for *Barentsia hildegardae* represent the first compelling demonstration of colony and genet gonochorism (mode GgG) in a kamptozoan. Earlier reports of colony gonochorism in the genus (Table I) were less reliable because, based as they were on isolated or brief observations of living colonies or scrutiny of fixed specimens, they could not eliminate the possibility of sequential hermaphroditism at any level. These studies also did not attempt to assess the sexual mode of whole genets.

Barentsia hildegardae evidently displays mode GgG. Calyces contained gonads of only one sex, and did not change sex over time in slide-grown colonies. Every one of the 200 slide-grown colonies contained calyces of only one sex; none changed sex over the one-year sampling period; those that survived through a second year remained the same sex as well. Male or female, the 70 replicate colonies of 7 genets also did not change sex over the entire sampling period.

Although slide-grown colonies of *B. hildegardae* provided unambiguous evidence for comprehensive gonochorism, the samples of colonies growing on ascidians (Fig. 3a) did not. Most of the 2-cm^2 plots were skewed heavily toward male or female calyces, but many contained a mix of sexes. I conclude that these ascidians hosted multiple colonies of *B. hildegardae* growing intertwined: each 2-cm^2 plot probably contained calyces mainly from one colony (and thus of one sex), but also contained a few calyces from adjacent colonies (sometimes of the opposite sex). This result highlights the importance of knowing colony boundaries; in this case, field sampling alone could not have distinguished mode GgG from mode HhG.

The more limited data for *Barentsia conferta, B. ramosa,* and *B. benedeni* suggest that these species are also comprehensively gonochoric (mode GgG). Field sampling was more strongly suggestive of colony gonochorism for *B. conferta* (Fig. 3b) and *B. ramosa* (Fig. 3c) than for *B. hildegardae* (Fig. 3a). Both *B. conferta* and *B. ramosa* grow more densely than does *B. hildegardae*, thus limiting the potential for intrusion by colonies of different genets. The 21 slide-grown colonies of *B. benedeni* had few sexually mature calyces, but the pattern (Fig. 3d) was consistent with colony gonochorism, as was the huge, wholly female preserved colony that I examined. At the

Figure 3. Patterns of sex distribution in five barentsiid kamptozoan species. For each species, all calyces from a plot, aggregation, or slide were sexed microscopically. Percent maturity is shown on the *y*-axis; plots, aggregations, or slides are shown on the *x*-axis and have been arranged by decreasing female maturity and increasing male maturity. (a) *Barentsia hildegardae.* Results from 40 (2 cm^2) plots on ascidians; a plot contained an average of 38 calyces. (b) *Barentsia conferta.* Results from 48 aggregations on coralline algae; an aggregation contained an average of 127 calyces. (c) *Barentsia ramosa.* Results from 33 aggregations on rocky overhangs; an aggregation contained an average of 269 calyces. (d) *Barentsia benedeni.* Results from 21 slide-grown colonies and one large preserved colony (represented by left-most bar); a slide contained an average of 46 zooids; the preserved colony contained 1035 calyces. (e) *Barentsia discreta.* Results from 21 slide-grown colonies; a slide contained an average of 30 calyces.

Sexual mode	Species	Reference
GgG	**B. benedeni**	Foettinger, 1887; Ehlers, 1890; Mariscal, 1965; Wasson, this paper
	B. conferta	Wasson, this paper
	B. discreta	Oka, 1895; Marcus, 1939
	B. gracilis	Foettinger, 1887; Marcus, 1939
	B. hildegardae	Wasson, this paper
	B. laxa	Marcus, 1939*; Toriumi, 1951*
	B. ramosa	Wasson, this paper
HhG	B. benedeni	Emschermann, 1994
	B. discreta	Ehlers, 1980; Mukai and Makioka, 1980; Emschermann, 1982; 1985; 1994; Wasson, this paper
	B. elongata	Emschermann, 1994
	B. gracilis	Emschermann, 1994
	B. matsushimana	Emschermann, 1982
HhH	**B. aggregata**	Johnston and Angel, 1940; Wasson, this paper
	B. laxa	Harmer, 1915†

The only reports that are based on repeated examination of the same colonies to determine colony (as well as calyx) sexual mode are those of Mukai and Makioka (1980), Emschermann (1985), and Wasson (this paper); the species examined by these authors are shown in boldface to emphasize that their sexual mode is fairly certain. The sexual modes of the remaining species are less certain, and some appear under two sexual modes in this list. For explanation of the three-letter abbreviations for the sexual modes, see Figure 1.

* The species identified as *Barentsia laxa* by Marcus and Toriumi is probably *B. elongata* (Emschermann, pers. comm.).

† The species identified by Harmer as *Barentsia laxa* is probably undescribed; his material (British Natural History Museum 1916.8.23.38) has distinctly annulated, tall zooids very different from those of *B. laxa*.

calyx level, gonochorism seems certain for all three of these species, and at the colony level, gonochorism seems very likely as well. However, replicate colonies of the same genet were not examined, so genet gonochorism has not been demonstrated. And the same colonies were not observed over time, so the possibility of sequential hermaphroditism cannot be entirely excluded, either.

The sexual modes of *B. conferta* and *B. ramosa* are described for the first time in this paper. There are conflicting reports about the sexual mode of *B. benedeni* (Table 1). Foettinger (1887), who described the species, was convinced that colonies as well as calyces are gonochoric, and Ehlers (1890) and Mariscal (1965) supported his view. However, Emschermann (1994) reported colony hermaphroditism via gonochoric calyces of both sexes

(mode HhG) for this species. My observations support the findings of the earlier investigators.

Mode HhG in Barentsia discreta

Mode HhG is much easier to demonstrate than mode GgG because the presence of gonochoric calyces of both sexes along the same or clearly connected stolons is the only evidence needed. Replicate colonies of the same genet need not be examined, because a genet consisting of simultaneously hermaphroditic colonies is necessarily simultaneously hermaphroditic itself. However, it is critical that male and female calyces be observed along the same stolon or on stolons whose structural continuity can be demonstrated, or that both sexes be observed in single colonies grown in isolation. Merely observing male and female calyces growing together in a clump does not suffice to identify mode HhG, because such juxtaposition may also result from the intertwined growth of gonochoric colonies (mode GgG) of both sexes, as in field samples of *B. hildegardae* (Fig. 3a). Already in 1890, Ehlers noted how difficult it is to determine the sexual mode of interwoven kamptozoan colonies.

The sexually mature colonies of *Barentsia discreta* clearly displayed mode HhG: gonochoric calyces of both sexes were simultaneously present in the same colonies (Fig. 3d). This contradicts earlier reports (Oka, 1895; Marcus, 1939) of colony gonochorism, but supports the findings of one older report (Ehlers, 1890, on *B. macropus* = *B. discreta*) and two recent, detailed studies (Mukai and Makioka, 1980; Emschermann, 1985) of sexual reproduction in *B. discreta* (Table 1). The sex of calyces of *B. discreta* is environmentally determined (Emschermann, 1985), and this sexual lability results in hermaphroditic colonies. The colony-level sexual mode is just the sum of its component parts: a colony built of calyces that have the potential to be either male or female is hermaphroditic (as in *B. discreta*), whereas a colony built of calyces with fixed sex, either male or female, is gonochoric (as in *B. hildegardae* and the other comprehensively gonochoric species).

Emschermann (1982, 1994) has reported mode HhG for four other barentsiid species (Table I).

Simultaneously hermaphroditic calyces: mode (HhH) overlooked

It is quite easy to demonstrate that a species is comprehensively hermaphroditic (mode HhH). Observations of mature ovaries and testes within the same calyx are sufficient. Examination of an entire colony or replicate colonies of the same genet is not required, because simultaneous hermaphroditism of the calyx necessarily implies simultaneous hermaphroditism of both the colony and the genet. It is also not essential to monitor calyces or colo-

nies over time, although that is certainly the best way to observe the timing of maturation and to detect tendencies toward protandry or protogyny.

It has been suggested that all *Barentsia* species have gonochoric calyces (Mariscal, 1975; Emschermann, 1994). Johnston and Angel (1940), however, reported hermaphroditic calyces of *Barentsia aggregata,* and my examination of their material confirms that calyces of this species often contain both mature testes and ovaries. Mode HhH thus is represented in the genus *Barentsia* (Table I).

Although many calyces were simultaneously hermaphroditic, justifying the designation of the species as HhH, some calyces appeared to be only male or only female. Perhaps a period of male maturity precedes simultaneous hermaphroditism, and a period of female maturity follows degeneration of the testes. Or, intriguingly, perhaps sex determination is so labile in this species that fully mature calyces can be either male, female, or hermaphroditic. To distinguish among these alternatives, living colonies must be observed over time.

Harmer (1915) reported hermaphroditic calyces in a kamptozoan from Indonesia that he identified as *Barentsia laxa* (but that almost certainly represents an undescribed species, with tall, flexible, deeply annulated rods). His illustration (pl. 2, fig. 11 in Harmer, 1915) of a hermaphroditic calyx is unconvincing; it appears to be a female with embryos. His material (British Natural History Museum 1916.8.23.38) is in such poor condition that I was not able to see ovaries and testes, so his report remains unconfirmed.

A diversity of sexual modes in the genus Barentsia

The suggestion that most or all species of kamptozoans are hermaphroditic (Nielsen, 1989) has been perpetuated in many invertebrate zoology textbooks (*e.g.,* Brusca and Brusca, 1990; Ruppert and Barnes, 1994). Within the genus *Barentsia,* hermaphroditic colonies with gonochoric calyces (HhG) were considered the rule (Emschermann 1985, 1994). However, the data presented here demonstrate that three sexual modes (GgG, HhG, and HhH) are expressed by species of *Barentsia,* and that comprehensive gonochorism (mode GgG) may be at least as common as HhG. In fact, I hypothesize, on the basis of a recent phylogenetic analysis of northeastern Pacific *Barentsia* species (Wasson, 1997), that comprehensive gonochorism is plesiomorphic for the genus, and hermaphroditism is derived.

What selective pressures might have fostered the evolution or maintenance of such contrasting modes of sex? Comprehensive gonochorism (GgG), as in *Barentsia hildegardae,* prevents the self-fertilization that might occur if calyces or colonies were hermaphroditic. Such forced outcrossing may be favored under stable environmental conditions and high population densities, where a mate of the opposite sex is always likely to be nearby. Mode HhG, as in *B. discreta,* may combine some advantages of gonochorism (*e.g.,* construction of more specialized reproductive structures) at the level of the calyx with some advantages of simultaneous hermaphroditism (*e.g.,* doubling the chance of encountering a mate) at the level of the genet (Ghiselin, 1969). Furthermore, a strategy of phenotypic sex determination of calyces (as in *B. discreta's* HhG) may be advantageous in unpredictable environments (Charnov and Bull, 1977) and under variable population densities. For example, a colony might continually adjust its production of male and female calyces in response to environmental cues, including local densities of male and female calyces in neighboring colonies. The calyx hermaphroditism (HhH) of the Antarctic *B. aggregata* may be favored under stringent environmental conditions in which the overall chance of fertilization is very low because the breeding period is short, growth is slow, and population densities are low. Under such conditions, when gametes of the opposite sex are only rarely encountered, calyx hermaphroditism may be a good strategy (Ghiselin, 1969). And simultaneous hermaphroditism may also allow for self-fertilization, if the benefits of any sex at all outweigh the costs of inbreeding. A taxon such as the genus *Barentsia,* in which closely related species have remarkably different sexual modes, would be an excellent model system for testing such hypotheses about the evolution of different colonial modes of sex, by mapping ecological data about environmental conditions, population density, and self-fertilization on a robust phylogenetic tree.

Comparisons with other colonial animals

Colonial cnidarians (hydrozoans and anthozoans) express all three sexual modes (GgG, HhG, and HhH) that barentsiid kamptozoans do (Fadlallah, 1983; Fautin, 1992). In addition, some colonial hydrozoans and anthozoans have mode HhS, in which sequentially hermaphroditic calyces are not synchronized in their sex change, so that the colony as a whole is simultaneously hermaphroditic (Wasson and Newberry, 1997). This mode has not yet been reported for a barentsiid kamptozoan.

Bryozoans and colonial hemichordates (pterobranchs) display two of the three modes (HhG, HhH) described for barentsiid kamptozoans, but apparently have no members with comprehensively gonochoric (GgG) colonies (Hadfield, 1975; Reed, 1991). Some bryozoans, like some colonial cnidarians, also exhibit mode HhS.

Colonial urochordates (ascidians and thaliaceans) overwhelmingly display one mode of sex also found in barentsiid kamptozoans, namely HhH (Berrill, 1975). A

very few urochordates reproduce by means of modes GgG, SsS. and HhS (Berrill, 1975).

The sexual mode of many colonial animals is still incompletely known. Many reports describe only the sexual mode of zooids, not of colonies and certainly not of whole genets. Few researchers have observed colonial animals over time, as is necessary to distinguish gonochorism from sequential hermaphroditism at any level; even fewer have looked at multiple colonies of the same genet, as is required to determine the genet's sexual mode. Only as the dynamics of sexual reproduction are thoroughly investigated at all three levels—zooid, colony, and genet— can we begin to understand the phylogenetic distribution of colonial sexual modes and the influence of evolutionary pressures on them.

Acknowledgments

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